

SMALL, J. The origin and development of the Compositae. *New Phytol. Reprint 2*: 1-334. *pls. 1-6*. 1919. [Reprinted from a series of papers in *New Phytol.* 16-18. 1917-1919.]

KEY TO GENERA OF SENECEONEAE IN THE SOUTHEASTERN UNITED STATES

- A. Heads radiate, or if discoid, the style branches truncate and only slightly penicillate; florets yellow (white or purple in *Senecio Rugelia* Gray).
- B. Leaves opposite; carpellate florets in two series; pappus uniseriate; style branches of perfect florets slightly acute with a brushlike tip of papillose hairs (penicillate). 1. *Arnica*.
- B. Leaves alternate; carpellate florets, if present, in a single series; pappus multiseriate; style branches of perfect florets truncate and more or less penicillate. 2. *Senecio*.
- A. Heads discoid; style branches always with a terminal appendage; florets white, purple, reddish, or if yellow-orange, the style branches exceedingly long and covered with papillose hairs.
- C. Florets white or whitish (pinkish in some *Cacalia*); style branches with a short conical appendage which has no hairs at the base or only a semi-circular crown of hairs.
- D. Leaves palmately nerved or pinnately nerved and hastate; corollas deeply 5-parted; all florets perfect. 3. *Cacalia*.
- D. Leaves pinnately nerved, oblanceolate to lanceolate, irregularly lobed; corollas shallowly 5-toothed; outer florets of head carpellate. 4. *Erechtites*.
- C. Florets lavender, red, or yellow-orange; style branches either with a long conical appendage surrounded by a circle of hairs or elongate and penicillate.
- E. Involucre of a single series of bracts; florets purple or flame colored; style branches with a conical appendage surrounded by a circle of hairs. 5. *Emilia*.
- E. Involucre with an outer series of supernumerary bracts; florets yellow-orange; style branches elongate and penicillate. [*Gynura*.]³

1. *Arnica* Linnaeus, *Sp. Pl.* 2: 884. 1753; *Gen. Pl.* ed. 5. 376. 1754.

Perennial herbs to 90 cm. tall arising from an erect and simple [or creeping and branched] rhizome covered with fibrous roots [or scales, or naked] and the remains of last year's leaf bases. Flowering stems herbaceous, bearing 2 or 3 [1-3 or 5-10] pairs of opposite, ovate to suborbi-

³ Although included in J. K. Small's *Manual of the Southeastern Flora*, *Gynura* Cass. has apparently not survived as an escaped herb. I have seen only two specimens, presumably those on which Small based his inclusion of *Gynura*, which seem to have been noncultivated (both were Florida: Palm Beach Co., Delray. Pineland. May 12, 1922. *J. K. Small 10497* [NY]). According to Dr. R. W. Long, there are no records of naturalized *Gynura* in Florida at the University of South Florida, and Dr. D. B. Ward has indicated that the University of Florida has only three specimens, all of which are from cultivation. In his "Compositae of South Florida" (*Quart. Jour. Florida Acad. Sci.* 14: 189. 1951), R. B. Ledin listed *Gynura aurantiaca* (Blume) DC. only as a cultivated species. The genus is nevertheless included in the key, and a number of pertinent references are among those for the subtribe.

cular [lanceolate] sessile [petiolate] leaves with multicellular filiform and/or glandular hairs. Inflorescence cymose (appearing paniculate in ours) of 1–30 campanulate, radiate, monochromatic heads, each with a ring of hairs at the top of the peduncle beneath the head. Involucre of 2 series of essentially equal herbaceous, lanceolate bracts with a variable pubescence; receptacle convex, fimbriate. Florets dimorphic; pappus white or straw colored, setose; ray florets carpellate [occasionally with 5 staminodia], the corolla with a 3-toothed ligule, yellow or orange; disc florets perfect, the corolla goblet shaped [tubular], yellow or orange; anthers of disc florets yellow [purple] with a lanceolate terminal appendage and short auricles at the base; style branches of perfect florets slightly flattened, with penicillate tips of long papillae. Achenes cylindrical with a ring at the base, surface with glandular hairs [or glabrous, or with both glandular and double hairs], shorter and broader in the ray florets than in the disc florets. LECTOTYPE SPECIES: *A. montana* L.; see Britton & Brown, *Illus. Fl. No. U. S. ed. 2. 3: 533. 1913.* (Name of uncertain origin, possibly either from Greek, *ptarmica*, goose-tongue, or *amicur*, friend, because the plant is used medicinally.) — LEOPARD'S BANE, WOLF'S BANE.

A genus of some 32 species in five subgenera (Maguire), represented in the southeastern United States only by *Arnica acaulis* (Walt.) BSP., $2n = 38$, of subg. ARNICA. This species reaches farther south than any other in the genus, occurring from southern Pennsylvania and Delaware in damp areas of the open pine forest of the Atlantic Coastal Plain to northern Florida. Other species of *Arnica* occur in quite different habitats in the tundra and mountains of higher latitudes. Three other species enter the eastern United States far to the north of our area: *A. lonchophylla* Greene subsp. *arnoglossa* (Greene) Maguire (subg. ARCTICA Maguire) in northern Minnesota, *A. cordifolia* Hook. (subg. AUSTROMONTANA Maguire) on the Keweenaw Peninsula of Michigan, and *A. lanceolata* Nutt. (subg. CHAMISSONIS Maguire) in the high mountains of Maine, New Hampshire, and New York. The remaining species are concentrated in northwestern North America but some are distributed in other boreal areas. However, only the polymorphic *A. alpina* (L.) Olin (subg. ARCTICA), considered the basal species of the genus by Maguire, is completely circumboreal. One of its six subspecies, *A. alpina* subsp. *tomentosa* (Macoun) Maguire, dips down the Rocky Mountains into Montana.

Our species, *Arnica acaulis*, shows a disjunct relationship with the northern European *A. montana* L., $2n = 38$, the only other member of subg. ARNICA (cf. Maguire). *Arnica acaulis* is not closely related to any of the other 30 species found in North America and is easily distinguished from them by its short, upright, unbranched rhizome covered with fibrous roots.

The generic affinities of *Arnica* seem to be rather obscure. Cassini tentatively placed the genus in his "Tagetinae" with a group of genera now considered to belong in the Heliantheae. Bentham first placed it in the

Senecioneae, remarking that, morphologically, it was not very close to *Senecio* L. but approached *Doronicum* L. in several characters. James Small also mentioned morphological similarities to *Doronicum*, but thought that "a relationship of *Arnica* with *Tussilago* L." (p. 284) was confirmed by the presence in *Tussilago* of faradiol, a sterol related to the arnidol found in *Arnica*.

Maguire supposed a North American origin for the genus since all five of the subgenera (except subg. ARNICA) are found in northwestern North America and the species there show few specializations compared with more peripheral species. A chromosome number report of $2n = 10$ (the lowest in the genus) for the northwestern American *Arnica longifolia* D. C. Eaton bolstered this view, but this count has subsequently been shown to be incorrect; $2n = 76$ (also reported as $2n = 60$) is now accepted as the correct count.

Chromosome numbers now known for more than half the species (representing all subgenera) include $2n = 38, 57, 60, 69, 76, 90 \pm 6, 95 \pm 4$, and ca. 97. These counts combined with other evidence prompted Ornduff *et al.* to postulate a base chromosome number of 19.

The occurrence of apomixis has complicated both the counting of chromosomes and the delimitation of species in *Arnica*. Afzelius first reported apomixis in three species in which there was no meiosis, no tetrad formation, and the production of the embryo sac directly from the megaspore mother-cell (apparently in both the ray and the disc florets). Recently, Baker listed autonomous apomixis for five additional species and the possibility of pseudogamy in two others. Four different species and the subspecies of two others which he investigated showed normal sexual reproduction. All species with a diploid number of 38 studied thus far are sexually normal; those with higher numbers (with one exception) are apomictic. Yet, a number of the species studied by Ornduff *et al.*, including several with a diploid number of ca. 38, exhibited irregularities in pollen meiosis.

Stamen irritability,⁴ or the reaction of the stamens and/or style to a stimulus when the floret is touched, was reported in *Arnica alpina* by Small.

Several species (*Arnica montana* L., *A. fulgens* Pursh, *A. sororia* Greene, and *A. cordifolia* Hook.) have chemicals useful in medicine. The heads are collected and dried, the florets removed and ground, and a tincture prepared from the powder. This liquid is used externally for cuts, bruises, and sprains, but can cause severe dermatitis. Small internal doses are used as a respiratory, nervous, and digestive system stimulant, diuretic, and purgative, but large doses can lead to central nervous system disturbances, vascular collapse, and even death.

⁴Stamen irritability is discussed by James Small in his Chapter III (see subtribal references). Two basic kinds are involved: that in which the style is exerted when the floret is touched, thus forcing out the pollen, and that which results in a contraction of anther filaments which tilts the floret toward the stimulus. Some species have florets capable of tilting in only limited directions. In *Arnica*, the anther tube (and consequently the floret) is capable of moving in any direction.

Historically, extracts have been made from either the dried rhizomes or the flowering heads, but only the heads are now used. The active principle is arnicin (apparently $C_{20}H_{70}O_4$), a yellow hygroscopic substance soluble in organic solvents and alkalies.

In this connection it should be noted that Hess found an intensely yellow-colored hygroscopic compound in the basal cells of the double hairs⁵ of *Arnica montana* achenes. Thus the substance used medicinally by man is possibly utilized in the plant for water absorption (and perhaps also as a deterrent to grazing animals). Interestingly, our species, *A. acaulis*, has no double hairs on the achenes and also has never been used for medical purposes.

The attractiveness of the large showy heads and the "alpine" habit of numerous species of *Arnica* have led to the cultivation of about a dozen taxa (see Dress).

REFERENCES:

Under subtribal references see BENTHAM, BENTHAM & HOOKER, HESS, ORNDUFF *et al.*, RICKETT, and SMALL (Chapter III).

AFZELIUS, K. Apomixis in der Gattung *Arnica*. Sv. Bot. Tidskr. 30: 572-579. 1936.

BAKER, W. W. Apomixis in the genus *Arnica*. (Abstr.) Am. Jour. Bot. 53: 636. 1966.

CASSINI, H. Note supplémentaire. Opusc. Phytol. 3: 201-207. 1826. [*Arnica*, 203.]

DRESS, W. J. Notes on the cultivated Compositae 2. *Arnica*. Bailey 6: 195-198. 1958.

FOURNIER, P. Plantes médicinales et vénéneuses de France. 3 vols. Paris. 1947. [*Arnica*, 1: 131-137.]

MAGUIRE, B. A monograph of the genus *Arnica* (Senecioneae, Compositae). Brittonia 4: 386-510. 1943. [Morphology, systematics, and evolution.]

SIMS, J. *Arnica montana*. Bot. Mag. 42: pl. 1749. 1815.

YOUNGKEN, H. W. Textbook of pharmacognosy. ed. 6. 1063 pp. New York. 1950. [*Arnica*, 875-880.]

2. **Senecio** Linnaeus, Sp. Pl. 2: 866. 1753; Gen. Pl. ed. 5. 373. 1754.

Caulescent perennial or annual herbs [shrubs, trees, or vines] with glabrous, tomentose, or villous stems and leaves. Leaves basal and/or alternate, entire, dentate, lobate, or pinnately parted; decreasing in size up the stem, the cauline often notably different from the basal ones. Inflorescence corymbiform [or monocephalous]. Involucre cylindrical or

⁵ Hess has studied in detail the morphology of the hairs of the achenes of numerous species of the Compositae representing all of the tribes. The hairs he calls double hairs (Zwillingshaare) consist of two more or less isometric basal cells which are surmounted by two perpendicular elongate and connate hair cells. The basal cells act as pulvini sensitive to water and raise the hair cells when absorption takes place. Numerous elaborations and/or reductions of this basic type of double hair have occurred in different species and genera of the family. (Cf. *Senecio*.)

hemispherical, composed of a single row [rarely more] of erect, usually free, flat [keeled], green bracts; supernumerary bracts sometimes present; receptacle slightly convex [flat], naked, foveolate. Florets dimorphic (perfect and carpellate) or all tubular and perfect; pappus setose-capillary, soft, white; ray florets, when present, carpellate, in a single outer series,⁶ the corolla with an irregularly toothed ligule, yellow; disc florets perfect, the corolla tubular, shortly 5-fid, yellow to orange (rarely white or light purple), the anthers with terminal appendages and truncate bases; pollen spherical, more or less spiny, prominently tricolporate (cf. Greenman); style branches of perfect florets truncate (to penicillate) or with a short, pointed apex. Achenes subterete, 5-10-nerved, variously pubescent. LECTOTYPE SPECIES: *S. vulgaris* L.; see Cassini, Dict. Sci. Nat. 48: 454. 1827. (Name Latin, applied to groundsel, *S. vulgaris*; derived from *senex*, old man, referring to the soft, white pappus which suggests the beard of an old man). — RAGWORT, GROUNDSEL.

An ubiquitous genus, possibly the largest of the flowering plants, estimates varying from 900 (Bentham & Hooker) to 3000 (Cabrera) species. There has been no treatment of the entire genus since that of De Candolle (1838) in which he divided the genus into several "series" based on geographical distribution. Most authors have arbitrarily accepted this treatment as a basis and have worked within one geographical area (e.g., Muschler, Africa; Cufodontis, northern Eurasia; Cabrera, Chile; Greenman, North and Central America). Greenman placed the North and Central American species in 21 sections; five sections (some of which are not very distinct) with eleven species occur in the Southeast and four introduced and 15 native species are known from the eastern United States as a whole.

The European section *SENECIO* (§ *Annui* Hoffm.), composed of weedy annual herbs, is represented in our area only by the now almost cosmopolitan *S. vulgaris* L., $2n = 40$, which differs from our other species in its annual habit and uniformly discoid heads of yellow flowers. Two species of sect. *SANGUISORBOIDEI* Greenman, characterized by the perennial habit of its species and the more or less glabrous, once or more pinnately parted leaves, occur in the Southeast. *Senecio glabellus* Poir., $2n = 46$, is wide ranging in wet habitats from Mexico eastward to Florida and north to Oklahoma, Kansas, Missouri, Illinois, Indiana, Kentucky, Tennessee, and North Carolina, whereas *S. Millefolium* Torr. & Gray (including *S. Memmingeri* Britton), with basal leaves two or three times pinnate, is restricted to rocks and cliffs in a few counties in the mountains of southwestern Virginia, western North and South Carolina, and northernmost Georgia. The remainder of the species of this section are found predominantly in the uplands of Mexico and Central America.

Most of our species fall into sect. *AUREI* Rydb., which is composed of

⁶ The presence of ray florets in normally radiate species is not an absolute character. The number of ray florets is also subject to great variation, mainly according to the number of involucre bracts.

perennial, usually glabrous herbs with petiolate simple or lyrate parted basal leaves and cauline leaves reduced upward. Six of the 22 species of this group reach our area: *S. aureus* L. (including *S. gracilis* Pursh), $2n = 44$; *S. Robbinsii* Oakes ex Rusby, $2n = 46$; *S. obovatus* Muhl. (including *S. rotundus* (Britton) Small), $2n = 40$; *S. Smallii* Britton, $2n = 44$; *S. pauperculus* Michx. var. *Crawfordii* (Britton) T. M. Barkley; and *S. plattensis* Nutt. *Senecio aureus*, *S. Robbinsii*, and *S. pauperculus* var. *Crawfordii* all frequent moist to wet meadows and bogs, *S. obovatus* and *S. plattensis* prefer drier areas, and *S. Smallii* grows primarily in fields, roadsides, and open woods. *Senecio Robbinsii* occurs in the Southeast only as a remarkably disjunct population on Roan Mountain (Tennessee-North Carolina border) with the principal populations located far to the north in the mountains of New York and New England and in adjacent Canada.

Many of these species commonly hybridize where their ranges and habitats overlap, which often makes identification of intermediate plants difficult. However, hybrids are usually restricted to "hybrid" habitats and do not seem to swamp out the parental species. The species of sect. AUREI, their ecology, natural history, and evolution, have been thoroughly discussed by Barkley.

Members of sect. TOMENTOSI Rydb. differ from those of sect. AUREI primarily in a tendency toward being permanently tomentose. The majority of the species are centered in the Rocky Mountains, but the range of the type species, *Senecio tomentosus* Michx. (including the glabrous-leaved f. *alabamensis* (Britton) Fern.; *S. alabamensis* Britton), $2n = 46$, stretches across the country in weedy areas from Arkansas and Texas to Florida and north to southern New Jersey. Hybrids between *S. tomentosus* and *S. aureus* are fairly common (Barkley), and the hybrid of *S. tomentosus* and *S. Smallii* also occurs. The latter has been studied cytologically (in the first meiotic division $2n = 21-22$ bivalents and 1-3 univalents). This evidence and other studies of Barkley have shown that some of the sections used by Greenman are artificial and should possibly be abandoned. In the southwestern United States (Colorado, New Mexico, Texas) hybrids are formed between *S. mutabilis* Greenm. (sect. TOMENTOSI) and *S. neomexicanus* Gray (sect. TOMENTOSI), *S. mutabilis* and *S. multilobatus* Torr. & Gray (sect. LOBATI Rydb.), and between *S. mutabilis* and *S. tridenticulus* Rydb. (sect. AUREI). An earlier study had already indicated that the species of the *S. multilobatus* group belonged in an integrated complex with species formerly considered to belong to sects. BOLANDERANI Greenm., LOBATI, and AUREI. (See also the cytological data of Ornduff *et al.*, 1967.)

The last section, RUGELIA (Shuttlew. ex Chapm.) Greenm., contains only the unique *Senecio Rugelia* Gray (*Rugelia nudicaulis* Shuttlew. ex Chapm.), winterwell, $2n = 56$, a perennial herb with alternate, undivided leaves and large, nodding discoid heads of white or light purple florets in a simple corymbose raceme. This species grows in partial shade in

cool woods (usually of *Picea rubens* Sarg. and/or *Abies Fraseri* (Pursh) Lindl.) at high elevations (ca. 1300 m.) in the Smoky Mountains of western North Carolina and eastern Tennessee. On the basis of both the morphology and the chromosome number, Ornduff *et al.* have reiterated that this species should be removed from *Senecio*.

Considering the size of the genus, relatively few studies have been made on its embryology, cytology, and anatomy. Palmblad (1965) and Ornduff *et al.* (1967) have recently added much new cytological information and discussed some of the possible significance of chromosome numbers within the genus, but too many species have still not been counted to allow decisions concerning the genus as a whole. Gustafsson reported no apomixis in the species of *Senecio* he examined, a finding corroborated on other species by Afzelius and Haskell. The breeding system in the few cases studied appears to be one of facultative outbreeding with occasional inbreeding (Knuth, Haskell). Hauman postulated that the arborescent senecios (sect. *ARBOREI* Hoffm.) of Africa are all obligate inbreeders.

Anatomical studies have been made most extensively on the African arborescent species of *Senecio* (cf. Hare). Recent comparative work by Carlquist with numerous other senecionid species has shown little correlation between wood anatomy and the classical infratribal taxonomy, apparently because in the Senecioneae stem anatomy is easily modified under different environmental conditions. Yet within *Senecio* itself, Carlquist found that clustering of species on the basis of wood anatomy was, in some cases, consistent with groupings based on other morphological criteria. Hare and Carlquist concur that the woody members of the Senecioneae are derived from herbaceous ancestors and that the stem structure of *Senecio* is advanced in comparison with other genera.

A recent study by Drury & Watson on some of the Eurasian sections of *Senecio* has revealed that the leaf and achenial hairs, pappus types, and the kinds of ovarian crystals — when carefully and critically examined — provide useful taxonomic characters. They call for a reassessment of many characters usually superficially examined in species of the Compositae and imply that the use of these characters might help in producing a more natural classification of such troublesome genera as *Senecio*.

The specialized anatomy of the achenial double hairs of *Senecio vulgaris* (see footnote 5 under *Arnica*) has been described by Macloskie and J. Small and that of several other species of *Senecio* by Hess. The basal cells, as in the double hairs of most Compositae, act as pulvini sensitive to moisture. In several species of this genus, the two hair cells are further specialized and are filled with a spiral tongue of a mucilaginous substance which is extruded when pressure due to water absorption forces the hair cells to separate. Apparently, the mucilage sticks the achenes to soil particles and thus helps to insure germination.

Alkaloids reported in at least 75 species (cf. Willaman & Schubert) undoubtedly account for the medicinal use of various species of *Senecio*.

In the United States, only *S. aureus* was extensively used, the leaves first being dried, then steeped in water, and the liquid used as a stimulant, diuretic, and uterine tonic. The last use of this brew by North American Indian women led to the common name of squaw-weed. In other parts of the world, shoots and leaves of several species are eaten raw or cooked. Some species (especially those of *Cineraria* L., if this genus is merged with *Senecio*) are cultivated as ornamentals.

Much attention has been directed toward *Senecio* and the Senecioneae because of the writings of James Small, who attempted to prove in an elaborate series of papers (1917–1919) that *Senecio* was the ancestral genus of the Compositae. His theory has, however, been dismissed by most workers with only a partial explanation. It thus seems worth noting here that four general concepts, now considered to be erroneous, lay at the base of his argument: (1) derivation of the Compositae from the Campanulaceae subfam. Lobelioideae; (2) acceptance of the now refuted Age and Area hypothesis of Willis; (3) the uplift of the Andes in the early Cretaceous; (4) belief in the doctrine of evolution by saltation. As a consequence of these tenets, Small proposed that the ancestral pre-Composite had a woody habit, a zygomorphic bilabiate corolla, and united anthers (free anthers are now considered primitive);⁷ that *Senecio*, the largest and most widespread genus of the family was naturally the oldest; that the uplift of the Andes in the Cretaceous (rather than in the Pliocene-Pleistocene as is now accepted) gave the genus ample time to spread around the world; and finally, that evolution by saltation, combined with this (presumed) early Andean uplift created a situation in which the lobelioid pre-Composite evolved and radiated as the Andes rose and thereby created a plexus of species able to migrate throughout the world.

Small also had a number of ideas concerning morphology which reinforced his conviction that *Senecio* was the ancestral Composite:

1. The pappus was developed from a structure that was morphologically a hair. Consequently, a fine capillary pappus (as is found in *Senecio*) should be primitive. The pappus now considered by most taxonomists to be the ancestral type is composed of broad, flat bristles resembling the lobes of the calyx, from which it is thought to be derived.

2. The inflorescence of the pre-Composite was an umbel with all of the pedicellar bracts except the outermost series already suppressed. Further reduction would have resulted in a head with a flat or convex naked receptacle and, correspondingly, a uniseriate involucre. Additional series of receptacular or involucral bracts would be produced by the abortion of florets in the head. Although it is still debated whether the primitive Composite possessed an umbel or a panicle, most authors now accept Bentham's view that receptacular bracts and a multiseriate involucre are unspecialized. A uniseriate involucre and a naked receptacle, as in *Senecio*, are now considered to be advanced reductions.

⁷ See Cronquist (1955) for a discussion of the evolution of the Compositae and an enumeration of characters considered to be unspecialized in the family.

3. Through a series of drawings, Small showed how all the types of style branches now found in the Compositae could be derived from the flat, truncated style arms of *Senecio*. Similarly, he derived all the anther types from the senecionid type with its terminal appendage and tailless base. Yet, since this kind of hypothetical derivation from a selected prototype can be made using almost any form (except for the obviously highly modified ones) as a starting point, it really has little biological meaning.

4. Several corolla characters in *Senecio* were also suggested by Small as primitive. Yellow, for example, was considered the "unspecialized" flower color. Bilabiate corollas found in the ray florets of some species of *Senecio* were deemed unspecialized because they were like those of *Lobelia*. Although yellow may be a basic flower color in the Compositae, the tubular corolla is now believed to be primitive and to have given rise to both the bilabiate and the ligulate corolla (cf. Koch).

5. The chromosomal evidence available to Small suggested that five was the base number for *Senecio*. More recent evidence, however, indicates that ten is actually the base number for the genus (Ornduff *et al.*).

In spite of these mistaken ideas about *Senecio*, Small's studies provide one of the most complete comparative morphological surveys ever made on the Compositae. Even without the bibliographies and summaries of previous work, his research is an indispensable reference on *Senecio* and the Compositae in general.

REFERENCES:

- All references listed under subtribe Senecioninae are pertinent.
- AFZELIUS, K. Embryologische und zytologische Studien in *Senecio* und verwandten Gattungen. *Acta Horti Berg.* 8: 123-219. 1924.
- ALEXANDER, E. J. *Senecio Rugelia*. *Addisonia* 20: 29, 30. pl. 655. 1937. *Senecio Millefolium*. *Ibid.* 31, 32, pl. 656.
- BARKLEY, T. M. A revision of *Senecio aureus* Linn. and allied species. *Trans. Kansas Acad. Sci.* 65: 318-408. 1962. [Excellent treatment of *Senecio aureus* species-group with comments on evolution.]
- . The intergradation of *Senecio plattensis* and *Senecio pauperculus* in Wisconsin. *Rhodora* 65: 65-67. 1963.
- . Taxonomy of *Senecio multilobatus* and its allies. *Brittonia* 20: 267-284. 1968. [Includes *S. Millefolium*, 275.]
- . Intergradation of *Senecio* sections *Aurei*, *Tomentosi* and *Lobati* through *Senecio mutabilis* Greenm. (Compositae). *Southwest. Nat.* 13: 102-115. 1968.
- CABRERA, A. L. El género *Senecio* en Chile. *Lilloa* 15: 27-501. 1949. [Includes 208 spp., numerous illustrations, little of generic or specific relationships.]
- CLUTE, W. N. The meaning of plant names. XLVII. *Senecios* and others. *Am. Bot.* 37: 105-109. 1931.
- COTTON, A. D. The megaphytic habit in the tree *Senecios* and other genera. *Proc. Linn. Soc. Bot. London* 156: 158-168. 1944.

- CRONQUIST, A. Phylogeny and taxonomy of the Compositae. *Am. Midl. Nat.* **53**: 478-511. 1955. [A general work on evolution of family with list of characters considered primitive and key to tribes.]
- CUFODONTIS, G. Kritische Revision von *Senecio* sectio *Tephroseris*. *Repert. Sp. Nov. Beih.* **70**: 1-266. *pls.* 1-5. 1933.
- DRURY, D. G., & L. WATSON. Anatomy and taxonomic significance of gross vegetative morphology in *Senecio*. *New Phytol.* **64**: 307-314. 1965.
- & ———. A bizarre pappus form in *Senecio*. *Taxon* **15**: 309-311. 1966. [Fluked pappus.]
- GREENMAN, J. M. Monographie der nord- und centralamerikanischen Arten der Gattung *Senecio*. *Bot. Jahrb.* **32**: 1-33. 1902. [A general treatment for this area, with discussion of anatomy, morphology, relationships, evolution, and key to sections.]
- . Monograph of the North and Central American species of the genus *Senecio* — Part II. *Ann. Missouri Bot. Gard.* **2**: 573-626. *pls.* 17-20. 1915; **3**: 85-194. *pls.* 3-5. 1916; **4**: 15-36. *pl.* 4. 1917; **5**: 37-107. *pls.* 4-6. 1918. [The basic treatment.]
- GUSTAFSSON, A. Apomixis in higher plants. *Lunds Univ. Årsskr.* II. Sect. 2. **42**: 1-68. 1946; **43**: 69-372. 1947.
- HARE, C. L. The arborescent senecios of Kilimanjaro: a study in ecological anatomy. *Trans. Roy. Soc. Edinb.* **60**: 355-371. 1940.
- HASKELL, G. Adaptation and the breeding system in groundsel. *Genetica* **26**: 468-484. 1953. [*S. vulgaris*.]
- HAUMAN, L. Les "Senecio" arborescents du Congo. Étude morphologique, phytogéographique et systématique. *Revue Zool. Bot. Afr.* **28**: 1-76. *pls.* 1-11. 1935. [Also includes photographs and comparisons with the páramos of S. Am.]
- KOCH, M. F. Studies in the anatomy and morphology of the Composite flower II. The corollas of the Heliantheae and Mutisieae. *Am. Jour. Bot.* **17**: 995-1010. *pls.* 51, 52. 1930.
- MACLOSIE, G. Achenial hairs and fibers of Compositae. *Am. Nat.* **17**: 31-36. 1883. [A short preliminary attempt, but interesting. For more detail, see Hess under subtribal references.]
- MUSCHLER, R. Systematische und pflanzengeographische Gliederung der afrikanischen *Senecio*-Arten. *Bot. Jahrb.* **43**: 1-74. 1909.
- ORNDUFF, R. Evolutionary pathways of the *Senecio lautus* alliance in New Zealand and Australia. *Evolution* **18**: 349-360. 1964.
- PALMBLAD, I. G. Chromosome numbers in *Senecio* (Compositae). I. *Canad. Jour. Bot.* **43**: 715-721. 1965. [65 collections representing 30 spp.; includes *S. antenariifolius* Britton, $2n = 46$, endemic to shale barrens of Virginia, W. Virginia, and Penn. to the north of our area.]
- SMALL, J. The pollen-presentation mechanism in the Compositae. *Ann. Bot.* **29**: 457-470. 1915.
- WILLAMAN, J. J., & B. G. SCHUBERT. Alkaloid-bearing plants and their contained alkaloids. *U.S. Dep. Agr. Tech. Bull.* **1234**: 1-287. 1961. [*Senecio*, 71-75.]

3. **Cacalia** Linnaeus, *Sp. Pl.* **2**: 834. 1753; *Gen. Pl.* ed. 5. 362. 1754.

Tall caulescent herbs arising from a rosette of alternate, petiolate, spathulate, ovate, reniform, or hastate, entire, undulate, crenate, or

toothed [or lobed] basal leaves; stem leaves petiolate or sessile, decreasing in size toward the inflorescence. Inflorescence a compound cyme of numerous campanulate discoid heads with cylindrical or campanulate involucre composed of a single series of herbaceous, lanceolate, winged or flat bracts (sometimes with an outer series of supernumerary bracteoles); receptacle flat, naked, or with a fleshy projection in the center. Florets monomorphic, perfect; pappus capillary, white; corolla deeply 5-cleft, white, cream, or pinkish; anthers with terminal appendages and obtuse bases; style branches truncate or with short conical [or elongate in some Mexican species] appendages. Achenes fusiform to cylindrical with a variable number of ribs, smooth. (*Synosma* Raf. ex Britton & Brown, 1898 [*Hasteola* Raf. ex Pojark., 1960, nom. superfluum]; including *Arnoglossum* Raf., 1817 [*Mesadenia* Raf., 1838, nom. superfluum].) LECTOTYPE SPECIES: *C. hastata* L., largely typified by the removal of the original species to other genera; see Miller, Gard. Dict. Abr. ed. 4. 1754; De Candolle, Prodr. 6: 327. 1838; Kitamura, Mem. Coll. Sci. Kyoto Univ. B. 16: 170. 1942; Shinnars, Field Lab. 18: 79. 1950; Pojarkova, Fl. URSS 26: 684. 1961.⁸ (Name from Greek, *kakalia*, a name given by Dioscorides to a plant believed to be a *Tussilago*.) — INDIAN PLANTAIN.

A genus of perhaps 40 species distributed from eastern Europe to eastern Asia, in eastern North America, Mexico, and Central America, and in South America along the Andes southward to Bolivia. The Mexican species were referred to *Psacalium* Cass., *Odontotrichium* Zucc., and *Pericalia* Rydb. by Rydberg (1924) and recently to these plus *Digitacalia* Pippen by Pippen (1968). Some Asiatic species have been removed to *Syneilesis* Maxim. and *Miricacalia* Kitamura. Nine species distinctly divisible into two sections occur in the southeastern United States. Section CACALIA (treated as the genus *Synosma* by Small and by Britton & Brown, ed. 2) is represented only by *Cacalia suaveolens* L., $2n = 40$, which occurs in moist woods from Massachusetts to Minnesota, southward to Missouri, Tennessee, and western North Carolina. Morphologically, it is distinct from all the other eastern North American species in having hastate leaves with pinnate venation, large heads with 12–15 involucre bracts (plus a ring of bracteoles), a naked receptacle, and numerous florets.⁹ Its affinities lie with the Eurasian *C. hastata* L., $2n =$

⁸The typification of *Cacalia* will be discussed in a subsequent paper. Rydberg (1924), Cuatrecasas (1960), and Pippen (1968), contrary to the course followed here, have maintained that *Cacalia* should be typified by *C. alpina* L., which was removed from *Cacalia* as the type species of *Adenostyles* Cass. This choice restricts the name to a genus of four or five species of Central Europe.

⁹I have seen one atavistic specimen of *Cacalia suaveolens* (Moore, Rosendahl & Hoff 19883, GH) with all normal leaves except for one reniform, palmately veined basal leaf. Moreover, the character of the fleshy projection in the center of the receptacle of sect. CONOPHORA and its absence in sect. CACALIA does not seem to be absolute. Some specimens of various species of sect. CONOPHORA seem to lack the fleshy growth.

60, and its Asiatic relatives rather than with any other North American species.

The seven other species in the Southeast form a closely knit distinctive group (cf. Pippen) which constitutes sect. CONOPHORA DC. (*Arnoglossum* Raf., *Mesadenia* Raf.). All are morphologically similar in having palmately nerved leaves, five involucral bracts, a fleshy projection in the center of the receptacle, and five florets.⁹ *Cacalia Muhlenbergii* (Sch.-Bip.) Fern. (*C. reniformis* Muhl.), $2n = 50$, occurs in woodlands from New Jersey and Pennsylvania, west to Minnesota and south to Missouri, Alabama, and Georgia. *Cacalia lanceolata* Nutt. var. *lanceolata*, $2n = 56$, occurs in moist to wet habitats from eastern Texas and Louisiana to Florida, northward into southeastern North Carolina, and *C. lanceolata* var. *Elliottii* (Harper) Kral & Godfrey (*M. Elliottii* Harper, *C. Elliottii* (Harper) Shinnery)¹⁰ occurs from peninsular Florida northward into South Carolina. *Cacalia diversifolia* Torr. & Gray also occurs in swampy areas of southern Georgia and northern Florida, westward to Louisiana, and *C. floridana* Gray is endemic to the dry, sandy oak and pine woods of central and northern Florida. *Cacalia atriplicifolia* L., $2n = 50, 52, 54, 56$, and *C. tuberosa* Nutt. (probably including *C. plantaginea* (Raf.) Shinnery), $2n = 54$, are wide ranging: the former in dry woodlands from New York to Minnesota and Nebraska, south to Oklahoma, and east to Mississippi, Alabama, and Georgia, and the latter in damp prairies from Ontario to Minnesota, south to Oklahoma and Texas. The last species of this section, *C. sulcata* Fern., is restricted to sandy bogs in southern Georgia and western Florida.

Within the North American species, evidence supports the distinctiveness of the two sections, but the inclusion of both into one genus. The morphological differences between the two groups of species are reinforced by differences in germination. Three species of sect. CONOPHORA which have been investigated (*Cacalia tuberosa*, *C. atriplicifolia*, and *C. Muhlenbergii*) have achenes which need four days to two weeks for germination and cotyledons which are strongly curved upon emergence. In contrast, *C. suaveolens* (sect. CACALIA) needs only 48 hours for germination and the cotyledons are only slightly curved when they emerge. Afzelius reported the infrequent occurrence of two embryo sacs in ovules of *C. suaveolens*, each formed from a separate megaspore mother-cell. In one sac, the egg apparatus was invariably crushed but the antipodals were normal,

¹⁰ The placement of *Cacalia ovata* Walt. is at present uncertain. This taxon, presumably distinguishable from *C. lanceolata* by its ovate, rather than lanceolate, leaves occurs from South Carolina to Florida. Apparently (cf. J. K. Small and Kral & Godfrey) all specimens referred by Chapman to this species are synonymous with *C. Elliottii* (Harper) Shinnery (= *C. lanceolata* var. *Elliottii* (Harper) Kral & Godfrey). *Cacalia* is not represented in Walter's herbarium (BM; photocopy, GH), and Walter's short description (Fl. Carol. 196. 1788) is hardly diagnostic. If *C. ovata* and *C. Elliottii* are eventually considered to be synonymous and if the present taxonomic treatment is followed, *C. lanceolata* var. *Elliottii* becomes *C. ovata* var. *ovata*, and *C. lanceolata* var. *lanceolata* will require under *C. ovata* a new combination based on the oldest legitimate varietal epithet (if available).

while in the other, the egg apparatus appeared normal, but the antipodals were crushed. Greene later reported that good seeds of *C. suaveolens* were difficult to find, and Wadmond stated that it was impossible to locate viable seed of *C. Muhlenbergii*. These two observations suggest a similar sort of meiotic irregularity in *C. Muhlenbergii*.

Another feature which links the Southeastern American species (sect. CONOPHORA) and the Asiatic species (sect. CACALIA) is the presence of the same type of asexual reproduction. Kral & Godfrey reported, as a general phenomenon in the Florida species, the production of lateral rosettes which become disconnected from the parent plant by disintegration of the connecting stolons. Liubarsky described the same phenomenon in greater detail for several Russian species. Two Japanese species, *Cacalia auriculata* DC. var. *bulbifera* Koidz. and *C. farfarifolia* Sieb. & Zucc., produce bulbils in the leaf axils (cf. Ohwi).

Within sect. CONOPHORA, the species are very similar morphologically, seemingly closely related, and apparently rather removed from other species in the genus. Hybrids within this section appear to be rare, however. The only natural hybrid reported, that between *Cacalia atriplicifolia* and *C. Muhlenbergii* (also produced artificially by Coleman), was exceedingly sterile (2-9 per cent pollen staining and no seed set).

Generically, *Cacalia* is ill defined from *Senecio* L. and its satellite genera. Originally, Linnaeus included in *Cacalia* the herbaceous perennials treated here (and other species) and a group of shrubby African plants now considered to constitute either the genus *Kleinia* Mill. or *Senecio* subg. *Kleinia* (Mill.) Hoffm. Bentham placed both the herbaceous and the shrubby groups in *Senecio*, while Hoffmann separated the two, retaining the herbaceous species as *Cacalia* and referring the species of *Kleinia* to *Senecio*. In opposition to Hoffmann's treatment, however, large and solitary crystals of calcium oxalate (rather rare in the Compositae according to Metcalfe & Chalk) have been found in both *Cacalia* and *Senecio* subg. *Kleinia*.

Chromosome numbers of the 27 species reported as *Cacalia* are $2n = 40, 50, 52, 54, 56, 58, 60, 70,$ and 120 . The 16 counts recently reported by Phippen as species of the segregate genera *Digiticalia*, *Odontotrichum*, *Pericalia*, and *Psacalium* are all $2n = 60$, with the exception of that for *O. Palmeri* which is $2n = \text{ca. } 50$. Ornduff *et al.* (1967) suggest that the basic chromosome numbers in *Cacalia* are 20 and 30 and that other numbers have been derived by aneuploid reduction from $n = 30$. More chromosome counts and further study of the generic limits of *Cacalia* on a worldwide basis undoubtedly are needed.

It seems possible, especially in view of the morphological continuity with *Senecio* in Africa, that the genus is of Old World origin, but Liubarsky's postulation of an origin in the region of the upper Amur River is highly questionable.

REFERENCES:

- Under subtribal references see BENTHAM, BENTHAM & HOOKER, DE CANDOLLE, HOFFMAN, ORNDUFF *et al.*, and RICKETT.
- AFZELIUS, K. Embryologische und zytologische Studien in *Senecio* und verwandten Gattungen. *Acta Horti Berg.* 8: 123-219. 1924. [*C. suaveolens*, 162.]
- ARANO, H. Cytological studies in subfamily Carduoideae (Compositae) of Japan XVII. The karyotype analysis in *Cacalia* and *Syneilesis*. *Bot. Mag. Tokyo* 77: 86-97. 1964. [Gives counts for 9 spp. of *Cacalia*.]
- COLEMAN, J. R. Natural and artificial hybrids of *Cacalia atriplicifolia* and *C. Muhlenbergii*. *Rhodora* 67: 55-58. 1965.
- CUATRECASAS, J. Studies on Andean Compositae — IV. *Brittonia* 12: 182-195. 1960. [Includes typification of *Cacalia*.]
- GREENE, E. L. Studies in the Compositae. — V. Part 3. The genus *Mesadenia*. *Pittonia* 3: 180-183. 1897.
- GREENE, H. C. Differences in achene characters and germination in some species of *Cacalia* L. *Am. Midl. Nat.* 39: 758-760. 1948. [*C. atriplicifolia*, *C. Muhlenbergii*, *C. suaveolens*, *C. tuberosa*.]
- HARPER, R. M. *Mesadenia lanceolata* and its allies. *Torreyia* 5: 182-185. 1905.
- HEMSLEY, W. B. *Cacalia tuberosa*. *Bot. Mag.* 131: pl. 8022. 1905.
- KITAMURA, S. Recognition of the genus *Syneilesis* Maxim. (In Japanese.) *Jour. Jap. Bot.* 10: 699-703. 1934.
- . *Les Cacalia du Japon*. (In Japanese.) *Acta Phytotax. Geobot.* 7: 236-251. 1938.
- KRAL, R., & R. K. GODFREY. Synopsis of the Florida species of *Cacalia* (Compositae). *Quart. Jour. Florida Acad. Sci.* 21: 193-206. 1958.
- LIUBARSKY, E. L. Notes on the genus *Cacalia* in the southern part of the Maritime Territory. (In Russian.) *Bot. Zhur.* 46: 98-102. 1961.
- METCALFE, C. R., & L. CHALK. Compositae. *Anat. Dicot.* 2: 782-804. 1950. [*Cacalia* and *Kleinia*, 786.]
- OHWI, J. *Flora of Japan* (in English). F. G. MEYER & E. H. WALKER, eds. ix + 1067 pp. Wash. D.C. 1965. [*Miricacalia*, 882; 13 spp. of *Cacalia*, 882-884; *Syneilesis*, 887, 888.]
- PIPPEN, R. W. Mexican "cacalioid" genera allied to *Senecio* (Compositae). *Contr. U.S. Natl. Herb.* 34: 363-448. 1968.
- POJARKOVA, A. Notae criticae de genere *Cacalia* L. s. l. (In Russian.) *Not. Syst. Leningrad* 20: 370-391. 1960. [Lectotype sp. = *C. atriplicifolia*; adopts *Hasteola* Raf. (ex Pojarkova) for *C. hastata*, *C. suaveolens*, and relatives.]
- . *Cacalia*. *Fl. URSS* 26: 683-697. 1961. [Lectotype sp. = *C. hastata* L.]
- RYDBERG, P. A. Some senecioid genera — I. *Bull. Torrey Bot. Club* 51: 369-378. 1924. [Includes incorrect typification of *Cacalia*.]
- SHINNERS, L. H. The Texas species of *Cacalia* (Compositae). *Field Lab.* 18: 79-83. 1950. [*C. plantaginea* and *C. lanceolata*, with comments on the application of the name *Cacalia*.]
- TAKESHITA, M. Cytological studies on *Cacalia* and its related genera. I. The chromosome number of three species and one variety of *Cacalia* and one variety of *Miricacalia*. (In Japanese.) *Jap. Jour. Genet.* 36: 217-220. 1961.*
- WADMOND, S. C. The Indian plantain. *Asa Gray Bull.* 6: 52. 1898. [*C. reniformis* = *C. Muhlenbergii*.]

4. *Erechtites* Rafinesque, Fl. Ludov. 65. 1817.

Robust annual [perennial] caulescent herbs with fibrous roots and alternate, toothed or parted, glabrous or pubescent leaves. Inflorescence a "panicle" or cyme of numerous heads, each with a basally swollen involucre composed of a single series of narrow lanceolate scabrous bracts often surrounded by a series of supernumerary bracteoles; receptacle flat, alveolate or fimbriate. Florets monomorphic and perfect [or in some cases florets dimorphic, the ray florets then carpellate with filiform 4-5-parted corollas]; pappus thin, white, soft, copious; corolla tubular, regular, 5-toothed, whitish or yellowish; anthers with obtuse bases; style branches of perfect florets with a terminal appendage of fused papillose hairs surrounded at the base by a semicircular crown of collecting hairs (cf. Belcher). Achenes oblong to linear in outline, more or less 10[-20]-ribbed, glabrous. (*Erechtites* sensu Bentham & Hooker and Hoffmann, in part.) TYPE SPECIES: *E. praealta* Raf. = *E. hieracifolia* (L.) Raf. ex DC. (Name from Greek, *Erechthites*, a name given by Dioscorides to a species of *Senecio*.) — FIREWEED, PILEWORT.

Two sections with five species native to the Americas (*sensu* Belcher) and adventive in the Pacific region, Asia, and Europe. One wide-ranging species, *Erechtites hieracifolia* (L.) Raf. ex DC., of sect. ERECHTITES (§ *Hieracifoliae* Belcher), occurs in weedy habitats in the southeastern United States.

Erechtites usually has been distinguished from *Senecio* and its allies by its two to several series of outer carpellate florets with filiform, eligulate corollas. Belcher, however, narrowed the genus to include only New World species which possess what he considers the diagnostic feature of the genus: style branches with an appendage of fused papillose hairs with a semicircular crown of collecting hairs at its base. He returned several Australian and Indonesian species traditionally included in *Erechtites* to *Senecio* and placed five New Guinean species (one population in New South Wales) in *Arrhenechthites* Mattfeld. The characters used to separate *Arrhenechthites* from *Erechtites* include the presence of functionally staminate disc florets and reduced, astigmatic (and thereby without the critical character of Belcher's *Erechtites*) style branches. In view of the obvious correlation between sterile (abortive) ovaries and reduced stigmas, the question arises as to whether these species are not simply inbreeders derived from the outbreeding American species. Also, the chromosome number of *Senecio* (*Erechtites*) *minimus* Poir., the only Old World species counted, has a diploid count of $2n = 60$, less like the most common number in *Senecio*, $2n = 40$, than *E. hieracifolia* with $2n = 40$. Regardless of which circumscription is used, the taxonomy of our species is unchanged.

Our species, *Erechtites hieracifolia*, has three varieties, two of which are now widely distributed weeds. Varietas *hieracifolia* (including vars. *intermedia* Fern. and *praealta* (Raf.) Fern.) occurs naturally from Can-

ada southward through the Greater Antilles. It is distinguishable from the other varieties by its short bracteoles less than 1/4 the length of the involucre and by its 10-ribbed achene. It has been introduced into Hawaii and Europe. Varietas *megalocarpa* (Fern.) Cronq. (*E. megalocarpa* Fern.), separable from var. *hieracifolia* in its much larger receptacle (twice as wide) and its 16–20-ribbed achene, is endemic to sandy coastal habitats from southeastern Massachusetts to New Jersey. Belcher's suggestion that the plants may be tetraploids derived from var. *hieracifolia* seems not to have been tested. The third variety, var. *cacalioides* (Fisch. ex Spreng.) Griseb., is found in Central America, the Lesser Antilles, and South America to Argentina, and is now established as a weed in Asia. It differs from the other two varieties in its longer bracteoles with multicellular hairs (instead of being glabrous or bearing unicellular hairs). Intermediates between this and var. *hieracifolia* occur in the West Indies.

The success with which *Erechtites hieracifolia* has managed to colonize new areas is apparently due to its adaptability to new environmental conditions and to its easily dispersed achenes. Ridley listed it as one of the first plants to recolonize Krakatau after the volcanic eruption of 1883.

Although this species is usually an annual herb, Carlquist has examined a Hawaiian specimen over six feet tall which had secondary xylem. The change from the annual habit in the Hawaiian population has occurred, Carlquist postulated, because plants on oceanic islands are "released" from the selection pressures of a cyclical climate. However, there must be some positive selection for woodiness on islands (see also Carlquist, 1965).

In Brazil, the leaves of *Erechtites hieracifolia* (and of *E. valerianifolia* (Wolf) DC.) are cooked with palm oil (Corrêa), and Ochse reports that in the East Indies the upper leaves, called "lalab," are eaten raw or steamed with rice and are rumored to be beneficial for nursing mothers.

REFERENCES:

- Under subtribal references see BENTHAM, BENTHAM & HOOKER, HOFFMANN, ORNDUFF *et al.*, and RICKETT.
- BELCHER, R. O. A revision of the genus *Erechtites* (Compositae) with inquiries into *Senecio* and *Arrhenechthites*. Ann. Missouri Bot. Gard. 43: 1–85. 1956.
- CARLQUIST, S. Wood anatomy of Senecioneae (Compositae). Aliso 5: 123–146. 1962. [Comparative anatomy with conclusions as to relationships within tribe and correlations with ecology.]
- . Island life. 451 pp. New York. 1965. [Chapter 8. Some remodeled plants.]
- COOPER, G. O. Cytological investigations of *Erechtites hieracifolia*. Bot. Gaz. 98: 348–355. 1936. [Describes both micro- and megasporogenesis.]
- CORRÊA, M. P. Dicionario das plantas uteis do Brasil e das exoticas cultivadas. 2 vols. Ministerio da Agricultura, Rio de Janeiro. 1926, 1931. [*Erechtites*, 2: 96. 1931.]

- FERNALD, M. L. The genus *Erechtites* in temperate North America. *Rhodora* 19: 24-27. 1917. [*E. hieracifolia*, its varieties, and *E. megalocarpha*.]
- OCHSE, J. J. Vegetables of the Dutch East Indies. 1006 pp. Buitenzorg, Java. 1931. [*Erechtites*, 132-134.]
- RIDLEY, H. N. The dispersal of plants throughout the world. xx + 744 pp. pls. 1-22. Ashford, Kent, England. 1930. [*Erechtites*, 133, 160, 656.]
- SANFORD, S. N. F. *Erechtites megalocarpha* in Rhode Island. *Rhodora* 28: 111. 1926. [See also H. K. SVENSON, *Rhodora* 41: 256. 1939.]

5. **Emilia** Cassini, Bull. Sci. Soc. Philom. Paris III. 1817: 68. 1817.

Annual or perennial caulescent herbs arising from a rosette of lyrate-pinnatifid or spatulate, dentate [entire], glabrous or glaucous leaves. Stem leaves alternate, dentate or lyrate-lobed, decreasing in size toward the lax corymbose inflorescence [plants sometimes monocephalous] of discoid heads. Involucre tubular, often swollen at the base, composed of a single row of lanceolate slightly scarious bracts; receptacle flat, naked. Florets perfect; pappus setose, soft, white or purplish; corollas tubular, shortly 5-fid, lavender [white] or red; anthers truncate at the base; style branches terete with penicillate appendages surrounded by a ring of hairs. Achenes 5-angled, truncate at both ends. TYPE SPECIES: *Cacalia sagittata* Vahl, nom. illegit. = *Emilia javanica* (Burm.) C. B. Robinson. (Derivation of name not explained but apparently from the French proper name Émilie.) — CUPID'S PAINTBRUSH.

A genus of about five species native to the Tropics of Africa and the Far East. Two weedy species, *Emilia sonchifolia* (L.) DC. ex Wight, $2n = 10$, and *E. javanica* (Burm.) C. B. Robinson (*E. coccinea* (Sims) G. Don in Sweet, *E. sagittata* (Vahl) DC., *E. flammea* Cass.), $2n = 20$, are naturalized in disturbed and weedy habitats in the warmer parts of peninsular Florida, where the latter is more frequently encountered. Both are also rather widely naturalized in the West Indies, Central America, northern South America, and Brazil.

The application of the names of these two species has been the source of much confusion. There has never been any doubt that there are two entities: one a species with lyrate-pinnatifid lower leaves, small heads, lavender (rarely white) corollas which barely exceed the involucre, lavender anthers and styles, and white pollen; the other with ovate-spatulate dentate leaves, carmine corollas which extend conspicuously beyond the involucre, orange anthers and styles, and bright yellow pollen. The first species is *Emilia sonchifolia*, and the other long has been known as *E. sagittata* in the Old World and *E. coccinea* in the New. When Cassini described *Emilia* he listed *Cacalia sagittata* Willd. as type species. Willdenow, in turn, referred to *Cacalia sagittata* Vahl, excluding the synonym *Hieracium javanicum* Burman. Because Willdenow excluded the synonym (Vahl's inclusion of this earlier legitimate name as a synonym made the name *Cacalia sagittata* superfluous) and because the type specimens of

Vahl's and Burman's names had not been examined, it has been assumed that two different taxa were involved. However, Mattfeld (1929) established that Vahl's type belongs to the large-headed, red-flowered species, and Fosberg (1966) finally located the Burman type and reported that it, also, was this species. Since Burman's is the oldest legitimate name available, it must replace the other names now used. That Cassini had the showy red-flowered species in mind when he described the genus *Emilia* is evidenced by his changing the name of the type species to *E. flammea* (nom. illegit.).

The two species apparently do not interbreed in nature, and attempts to produce artificial hybrids (cf. Lee) have failed, indicating that a sterility barrier (as well as the difference in chromosome number) is involved. The two species are not only incompatible, but also have different mechanisms of reproduction (at least in Jamaica): *Emilia sonchifolia* is an obligate inbreeder, while *E. javanica* is outbreeding.

The genus seems to be a natural group of species closely related to, but distinct from, *Senecio* L. Three of the five species counted have a chromosome number of $2n = 10$, and the other two have $2n = 20$. The species with five pairs of chromosomes are annuals apparently derived from less specialized species with $2n = 20$ (cf. Ornduff *et al.*).

The genus has no true commercial value, although *Emilia javanica* is sometimes used in tropical areas as an ornamental. Baldwin mentioned that the plants were eaten in the Far East, but not in the New World.

REFERENCES:

- Under subtribal references see BENTHAM, BENTHAM & HOOKER, DE CANDOLLE, HOFFMANN, and RICKETT.
- BALDWIN, J. T., JR. Cytogeography of *Emilia* Cass. in the Americas. Bull. Torrey Bot. Club 73: 18-23. 1946.
- . Cytogeography of *Emilia* in West Africa. *Ibid.* 76: 346-351. 1949.
- FOSBERG, F. R. Miscellaneous notes on Hawaiian plants. Occas. Pap. Bishop Mus. 23: 129-138. 1966. [Typification of *Emilia sagittata* Vahl and *Hieracium javanicum* Burm.]
- GARABEDIAN, S. A revision of *Emilia*. Bull. Misc. Inf. Kew 1924: 137-144. 1924.
- GOODING, E. G. B., A. R. LOVELESS, & G. R. PROCTOR. Flora of Barbados. 486 pp. London. 1965. [*E. sonchifolia*, 437, fig. 27.]
- KOSTER, J. Notes on Malay Compositae III. Blumea 7: 288-291. 1952. [Discusses application of names *E. sagittata* and *E. javanica*; but see Fosberg.]
- LEE, B. Jamaican species of *Emilia*. Sci. Notes News Jamaica 2: 14, 15. 1966. [Breeding systems of *E. sagittata* and *E. javanica*.]
- MATTFELD, J. Die Compositen von Papuasien. Bot. Jahrb. 62: 386-451. 1929. [*Emilia*, 443-447, nomenclature.]
- SIMS, J. *Cacalia coccinea*. Scarlet-flowered *Cacalia*. Bot. Mag. 16: pl. 564. 1802. [*E. javanica*.]

THE ARNOLD ARBORETUM
OF
HARVARD UNIVERSITY

Present address: THE GRAY HERBARIUM
OF
HARVARD UNIVERSITY

ASPECTS OF THE COMPLEX NODAL ANATOMY OF THE DIOSCOREACEAE¹

EDWARD S. AYENSU

THIS PAPER IS AN ATTEMPT to explain how the vascular tissue of two successive internodes maintains continuity in the complex nodal structure between them in stems of the Dioscoreaceae, especially in the genera *Dioscorea* and *Tamus*. Because of the economic importance of this family early emphasis (Mason, 1926) was placed on the relation between structure and function. This led physiologists to take a look at the anatomy before they had a full knowledge of how food substances are translocated in the plant.

The Dioscoreaceae is a monocotyledonous family which is distributed throughout the tropics and subtropics of the world. It is, by all standards, one of the most economically important foodstuffs in the diet of most tropical peoples (cf. Coursey, 1967). Attention has recently been focused on this family, especially the genus *Dioscorea*, because a precursor of cortisone and other related steroidal drugs is derived from the tubers of some species.

The unique anatomy of the nodes of the stems of the Dioscoreaceae was brought to attention by Mason (1926) when he studied the rate of sugar transport in *Dioscorea alata* L. Earlier, Falkenberg (1876) had called the glomerulus of the node an imperfect knot in his study of *D. villosa* L. Mason noted that the phloem was of a markedly abnormal type. He further observed that the sieve tubes of the successive internodes did not join with each other directly but through a glomerulus which was composed of a great number of oblong thin-walled parenchymatous cells, each with a distinct nucleus, running fairly parallel with each other. Behnke (1965a) questioned the presence of nuclei in the glomerulus cells. Present studies show that nuclei occur at certain stages in the ontogeny of these cells (FIG. 2).

In his study of the ontogeny of the stem of *Tamus communis* L., Burkill (1949) disproved Mason's claim that glomeruli were absent from the nodes of *T. communis*. Present studies reveal that glomeruli are certainly present in the nodes of *Tamus* (FIG. 12) and, although they cannot be easily overlooked, it should be emphasized that the glomeruli in this genus are not so pronounced as those of most species of *Dioscorea* (FIGS. 4-11).

¹ A full account of the vegetative anatomy of the Dioscoreaceae will be included in the *Anatomy of the Monocotyledons. Dioscoreales*, ed. C. R. Metcalfe, Oxford University Press.

Happ (1950) wrote his thesis on the nodes of the Dioscoreaceae but a copy is not available to me. However, a comment on it appeared in Braun's (1957) work. Essentially, Happ investigated by means of serial sections the interlacing of the xylem-phloem glomeruli in the vascular system of the node.

Brouwer (1953) published his account of the arrangement of the vascular bundles in the nodes of Dioscoreaceae and presented a diagram of the elements of the node. Brouwer concluded that the sieve tubes of two successive internodes were connected in the following manner: sieve tubes, funiculus cells, bast tubulus cells, glomerulus cells, bast tubulus cells, funiculus cells, and sieve tubes. Brouwer, following Mason (1926), concluded that the phloem-glomerulus cells were (a) densely filled with cytoplasm; (b) with a persistent nucleus with nucleolus; and (c) without sieve areas.

A comprehensive study of the nodal anatomy of *Dioscorea batatas* Decne. and *Tamus communis* was conducted by Braun (1957). He concluded that (a) the xylem-glomerulus consists of very numerous short tracheids of various sizes, the orientation of which is difficult to trace; (b) the phloem-glomerulus, which is divided into several partial glomeruli, is composed of a new type of translocatory cell, called phloem-glomerulus cells; and (c) the phloem-glomerulus cells possess thin walls without sieve pores and without visible pitting; they are distinguished from parenchyma cells by their lack of starch. Behnke's (1965c) electron microscopic studies show that sieve areas are, in fact, present in the phloem-glomerulus cells.

The present study, involving more species than were available to earlier investigators, essentially supports and extends their conclusions.

MATERIALS AND METHODS

My observations are based on 180 specimens of 112 species. A complete list and citations are given elsewhere (Ayensu, 1966).

Most of the specimens examined were fluid-preserved in formalin acetic alcohol. Microscopic details were studied in serial sections at 10μ , and those produced on a sliding microtome usually at 16μ . Depending upon the nature of some specimens, sections were cut up to 90μ . The sections were stained in safranin and counterstained with Delafield's haematoxylin followed by conventional differentiation, dehydration, clearing in xylene, and mounting in Canada balsam.

NODAL ANATOMY

As pointed out in an earlier paper (Ayensu, 1965), the vascular strands between the petiole and the stem at the nodes of many species of Dioscoreaceae are highly distinctive and are believed to be unique in the family. Longitudinal serial sections of the node reveal two groups of interlacing vascular elements, each forming a plexus close to the petiole insertion.